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Under the Reign of the Pea King (*Pisum sativum* L.): The Difficult Fate of the First Genetical Object[1]

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Abstract—The pea (*Pisum sativum* L.) is an important grain, vegetable, and forage crop, capable of improving soils via symbyotic nitrogen fixation. It is very important for Russia as a crop adapted to high latitudes and a cheap source of plant protein. At the same time, the pea is the first genetical object as used in G. Mendel's famous experiments. The first translocation in the history of genetics was also found in pea. The pea's generation time may be shortened to 35 days, which is comparable to *Arabidopsis*. Small and scarcely recognisable chromosomes hampered the development of cytogenetics in pea, while the recombination genetic maps remained inadequate until the 1990s and were improved only with the aid of molecular methods. To date, in the pea, two different numeration systems coexist for the linkage groups and the chromosomes as cytological objects. Recently the whole range of modern molecular methods markers of genetic analysis was applied to the pea, including isozymes; RAPD-, SSR-, RFLP-, AFLP-, STS-, CAPS-, sCAPS-, and SNP-markers; and also the methods of reverse genetics, including TILLING and virus-induced genomic silencing. Application of association mapping is expected to be applied. Several transcriptome studies were carried out on the pea. At the same time, the complete nuclear genome of the pea has not been sequenced but is expected to be sequenced in 2016. The synteny of the pea's genome to the sequenced genome of *Medicago truncatula* is actively used to work out new molecular markers in the pea. Genetic transformation is very difficult in the pea. The pea was used as an experimental model for investigating the following fundamental issues: genetic control of symbiosis with nitrogen fixing bacteria, influence of variation in the histone H1 gene on the phenotype, the mechanism of the nuclear-cytoplasmic conflict in remote crosses, the origin of B-chromosomes in plants, and the genetic control of the compound leaf morphology.

Keywords: Pisum sativum L., pea, genetical object, genetical maps, molecular markers

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The pea is one of the most cold-resistant pulse cultures grown in northern Russia. The global production of the pea grain comprised 10.4 Mt in 2009, being exceeded only by the kidney bean (Smýkal et al., 2012). The legume cultures remain practically the only source of plant protein, which comprises 23–25% of the dry seed mass in the pea (Bastianelli, 1998). In the future, the pea may become extremely important for the food security in Russia, the largest country in the world, since most of Russia's territory occupies high latitudes.

The pea is a unique culture and can be used in three main ways: as a vegetable, grain, and fodder. Perhaps, four ways of use would be more correct, since the roots of the pea bear nitrogen-fixing nodules, which are the best natural soil fertilizer; thus, the use of the pea in crop rotation to some extent restores the fertility of the soils.

It is no surprise that the pea is one of the most ancient cultures and the oldest genetical object. However, it is surprising how the genetical studies of the pea, despite being the first genetical studies in the world, were left behind by studies on other organisms and are catching up with them only recently. Perhaps the reason for this strange situation is the fact that since the second half of the twentieth century (after the Second World War), the progress of science shifted to lower latitudes, where the United States is located, while in the warmer climatic conditions the pea is less important than the more productive and culinarily more attractive kidney bean and soya bean.

THE PEA AS A GENETICAL OBJECT

When a universally educated (albeit, still without a diploma) Augustinian monk, Gregor Mendel, decided to go in for hybridisation and study heredity, he started from a thorough choice of the object of study. On the

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[1] The article was translated by the author.

Internet, one can find information (more as a network legend with the sources missing), that he turned his cell into a pets' corner, where he crossed various plants and even mice. It appears that he chose his object unhurriedly and thoughtfully (hawkweed (*Hieracium*) and honeybee became his study objects after the pea). The famous experiments with peas, which Mendel carried out over a period of 8 years and during which he grew at least 12980 plants (as mentioned in his epoch-making paper (Mendel, 1866) although probably considerably more in fact), were started in 1856. However, the pea was involved in the scope of Mendel's interests at least two years earlier, as in 1854, he wrote to his biology tutor that the pest pea weevil (*Bruchus pisorum* L.) hibernates in a pea seed rather than in the soil, and lays eggs on a young pod rather than in a flower. Anyway, an object fitting Mendel's goal was very luckily selected: there were a number of contrasting forms at his disposal which exhibited a great variety of external characteristics with respect to which these forms were steady in self-breeding but were easily crossable with each other. The pea was an annual plant allowing to get a generation per year, which is a great advantage over perennial plants, including trees and bushes, used in the experiments by Mendel's predecessors and contemporaries. It is worth mentioning here that the potential of the pea as a plant object with a short generation time in fact appeared much greater. For instance, a team headed by V.A. Berdnikov selected, as F23 of the cross accession VIR 7036 (Nepal) × Avanti cultivar, a miniature and very early ripening Sprint-1 line with the generation time in micro-greenhouse conditions of 32–35 days (Shumny, 1987), which is comparable to the "plant Drosophila", arabidopsis (*Arabidopsis thaliana* L. Heynh.). The result of Mendel's lucky choice is well known: it allowed him alone to found the science of genetics (while hawkweed and honeybee appeared less fruitful due to the peculiarities of their reproduction, unknown to Mendel, see Nogler, 2006).

The pea served as a basis for another important genetical discovery: it was the pea in which, for the first time in genetics, S. Hammarlund (1923) found a translocation—moreover, he did so by purely genetic methods, based on the data on the linkage of genes. Soon this translocation was visualised in the meiosis prophase by A. Håkansson (1929).

Later on, the pace of genetic studies on the pea slowed. One of the reasons for this was—however strange it seems in view of the above-mentioned discovery—the drawback of the pea as a cytogenetic object, as its chromosomes are very small and poor in terms of their morphological peculiarities.

The first good analysis of the pea karyotype was carried out by L.A. Levitsky (1931). Two of the seven chromosomes of the haploid set of the pea have satellites (Pellew, Sansome, 1932; Sansome, 1933), while the others lack any characteristic features and visually are very alike each other. Based on the relative length (related to the total length of the karyotype) of the chromosomes and their arms, S. Blixt (1958) managed to suggest an identification key for all the seven mitotic chromosomes; however, the two smallest chromosomes 1 and 2 still cannot be identified reliably (Hall et al., 1997). It is not possible to identify the meiotic chromosomes prior to the second division of meiosis, which is analogous to mitosis. With the poor recognition of chromosome, the cytogenetic studies on the pea were carried out only with the use of translocations (Sansome, 1932, 1933, 1938; Lamm, 1951, 1977; Lamm, Miravalle, 1959), the standard set of which was suggested by Robert Lamm (Lamm, 1951, 1977; Lamm, Miravalle, 1959). In the mid-1980s and with much effort, Donald Folkeson (1984a) managed to apply to the pea the method of differential staining. However, the result was not impressive as the differential staining was not particularly distinct. One and half decades later, the FISH technologies were applied to the pea's mitotic chromosomes, so that the ribosomal RNA clusters and microsatellites were visualised on them (Fuchs at al., 1998; De Martino et al., 2000; Neumann et al., 2001).

It seems that the lucky features of the pea as an object for the hybridological analysis of the inheritance of characteristics, that is, as it later became habitual to speak, for 'classical genetic analysis', so fruitfully noticed by Mendel, would soon lead to the detailed recombination genetic maps being worked out. Paradoxically, this problem was solved only in the 1990s and only through involving molecular markers. The first genetic map, including six linkage groups was compiled by S. Wellensiek (1925). However, Herbert Lamprecht (1948, 1953, 1954, 1955, 1957, 1961) was the scientist who played the main role in the construction of the entire genetic map of the pea, including seven linkage groups (with $n = 7$). By the 1970s, his genetic map was substantially updated with genes with external phenotypical manifestations, the number of which reached 169, which covered the map quite densely and made it appear quite pretty (Blixt, 1972).

However, in the 1980s–1990s, it turned out that that map was inadequate. Its different fragments appeared incorrectly combined in the linkage groups because of the overestimation of the reliability of the data indicating a distant linkage, which in fact were statistical artifacts. This was first found by the above-mentioned Folkeson (1984b, 1990a, b). Further repositioning of the fragments of Lamprecht's map was connected with mapping the *gigas* gene by Ian Murfet (1990), and the *His7* (Kosterin, 1992, 1993) and *bulbosus* (Kosterin, Rozov, 1993) genes by the author of this paper.

EXPANSION OF MOLECULAR METHODS

Soon the pea genetic map was updated with molecular markers, namely:

isozyme coding genes (Weeden and Marx, 1987; Hoey et al., 1996; Baranger et al., 2004);

random amplified polymorphic DNA sequences (RAPD-markers) (Hoey et al., 1996; Lu et al., 1996; Laucou et al., 1998; Rameau et al., 1998; Cheghamirza et al., 2002; Baranger et al., 2004);

microsatellite markers or simple sequence repeats (SSR-markers) (Lu et al., 1996; Baranger et al., 2004; Loridon et al., 2005);

polymorphic for their length fragments of DNA restriction (RFLP-markers—restriction fragment length polymorphism);

the same fragments but amplified after linking the adapters (AFLP-markers) (Lu et al., 1996);

DNA fragments amplified with random primers and polymorphic for restriction sites (STS-markers) (Lu et al., 1996; Weeden and Boone, 1999);

polymorphic sites of retrotransposon insertions (RBIP-markers—retrotransposon-based insertion polymorphism) (Ellis et al., 1998; Vershinin et al., 2003; Jing et al., 2010);

amplified fragments of coding genes, polymorphic for the presence of restriction sites (CAPS-markers—cleaved amplified polymorphic sequences; sometimes called EST-markers if worked out based on EST-sequences, which overcomplicates the nomenclature of the markers) (Gilpin et al., 1997; Konovalov et al., 2005); and

nucleotide substitutions in specific positions (SNP-markers—single nucleotide polymorphisms) (Aubert et al., 2006; Deulvot et al., 2010; Bordat et al., 2011).

This checklist can be updated with some more classes of molecular markers mentioned in the literature on the pea:

SSR-EST-markers—based on short tandem repeats inside gene coding parts (Bordat et al., 2011; Decarie et al., 2012);

SCAR- or STS-markers (sequence-characterised amplified regions, sequence tagged sites) (Rameau et al., 1998)—based on RAPD-markers, but with the further design of markers specific to a given fragment;

dCAPS-markers (derived CAPS) (Aubert et al., 2006)—analogous to CAPS-markers; however, a restriction site is absent from the analyzed DNA, but present in an imperfectly homologous primer.

New methods are appearing so rapidly that their terminology can barely keep pace.

In the past few decades because of the progress of the high-throughput sequencing methods allowing simultaneous analysis of any number of markers in a given sample (Deulvot, 2010; Bordat et al., 2011), the studies directed at constructing genetic maps and mapping the loci associated with valuable traits largely turned to the use of SNP-markers in coding sequences (Jing et al., 2007; Smýkal et al., 2012). Methods of genetic mapping are being swiftly developed and the present moment is not the best for reviewing them.

The number of molecular markers located on the pea genetic maps is growing explosively. The genetic map constructed by Loridon et al. (2005) included 229 SSR-markers, of which 13 were inside the coding sequences and the rest in the noncoding DNA. The maps obtained by a French team, with the predominant use of markers associated with coding genes, subsequently included 363 markers (111 inside the coding sequences) (Aubert et al., 2006), 536 markers (214 in the coding sequences) (Bordat et al., 2011) and, lastly, 2070 markers (Duarte et al., 2014). An independent team of Spanish researchers obtained a map including 416 markers in the coding genes (Carrillo et al., 2014).

Estimates of the total length of the pea recombination genetic map vary by a factor of 1.5: 937 cM (Weeden et al., 1998), 1132 cM (Carrillo et al., 2014), 1255 cM (Duarte et al., 2014), 1389 cM (Bordat et al., 2011), 1430 cM (Loridon et al., 2005), and 1458 cM (Aubert et al., 2006). The first estimate was assumed to correspond to the total number of chiasmata observable cytologically, while the dispersion of the estimates was explained through a number of artifacts (Knox and Ellis, 2001, 2002). However, one should not rule out possible genotype-dependent differences in the overall recombination intensity (Smýkal et al., 2012). There do not appear to be any data on the variability of the total number of chiasmata in the pea.

The preferable use in most recent studies of SNP-markers associated with coding sequences to some extent has resulted in a return to the situation when a genetic map contained mostly functional markers with phenotypic manifestation. However, the huge number of markers makes it difficult both to graphically present the mapping results and to apply the maps in practice.

Note that many molecular genetic maps were constructed disregarding the classical ones. Too few markers with a visible phenotypical manifestation were involved in the molecularly studied F2 populations and series of recombinant inbred lines. With progress and price reduction (unfortunately not in Russia) of the modern methods of high-throughput sequencing, a situation emerged when different research teams *de novo* construct very detailed maps with dense marker coverage for solving their specific goals with their specific material (populations of the second and third generations of crosses or, more frequently, of recombinant inbred lines, RIL). For instance, such was the work by Carrillo et al. (2014) who, in order to map the genes of quantitative traits (QTLs) associated with resistance to the ascochyta blight, have analyzed the set of recombinant inbred lines obtained from a single cross and constructed a map including 416 markers connected to the nucleotide substitutions in the coding sequences, of which 117 have been added *de novo*.

The problem of integrating new mapping data with the data obtained earlier and compiling a universal genetic map of the pea was recognised from the very onset of the use of molecular markers. Considerable efforts were made towards its solution (Gilpin et al., 1997; Weeden et al., 1998; Aubert et al., 2006; Bordat et al., 2011; Decarie et al., 2012; Smýkal et al., 2012). Thus, Bordat et al. (2011) used the data on 6 different populations of recombinant inbred lines obtained from crosses of 6 accessions and reported a consensus genetic map with 180 SSR-markers, 133 RAPD-markers, 6 RFLP-markers, and 214 markers associated with coding genes, but only 3 morphological markers. A later map of the same team (Duarte et al., 2014), based on 4 RIL populations, included 730 markers mapped earlier.

Along with the recombinant inbred line approach, a new approach appeared, which is expensive and indirect but fast; it was first worked out on a human being, a difficult genetic object, and received the name "association mapping" (Zhu et al., 2008). It implies indirect mapping, not involving crosses and hybrid populations, based on the analysis of the association of the characters and markers in huge data arrays of genotyped and phenotyped material. This approach is limited by factors such as the relatedness of the material studied and the density of the existing markers. No such works have so far been carried out for the pea; however, a preliminary evaluation of the data available suggested their aptitude for such a program (Jing et al., 2007).

OLD DEBTS

One has to acknowledge that presently the particular genetics of the pea in its classical sense—locating genes with a known function and/or phenotypic manifestation on the universal genetic map for the object—are in decline. One of the aspects of this decline is the conservation for 19 years of a regrettable situation when the linkage groups of the recombination genetic map and the chromosomes as cytogenetical entities have a different numeration. This problem was formulated and both numeration systems were used in parallel in the paper by S. Temnykh and N. Weeden (Temnykh and Weeden, 1993). The reason for preserving this situation in that moment consisted in insufficient confidence in the integrity of some linkage groups, which was expressed in sections with dashes and gaps in linkage groups I, IV, and VII of the genetic map published in the same issue of the journal Pisum Genetics (Ellis et al., 1993). Since then, however, 7 linkage groups of the pea have been revealed with certainty. Difficulties remain in the cytological identification of the two smallest chromosomes (Hall et al., 1997; Smýkal et al., 2012). However, their identification is now possible via FISH-technologies, in particular using the PisTR-B probe (Fuchs et al., 1998; Neumann et al., 2002). Hence, the actual mutual correspondence of the two systems of numeration—of chromosomes (traditionally denoted with Arabic numerals) and linkage groups (denoted by Roman numerals)—was established quite long ago: 1 = VI, 2 = I, 3 = V, 4 = IV, 5 = III, 6 = II, 7 = VII (Fuchs et al., 1998; Ellis and Poyser, 2002; Smýkal et al., 2012). However, such a long-anticipated act of renumeration of one of these systems according to the other system has not been done, apparently due to the inability to reach consensus in a problem worthy of Buridan's donkey: which of the two to choose (Smýkal et al., 2012).

Meanwhile, the persistence of two parallel nomenclatures has resulted in real problems. Thus, L. Fuzhong and S.A. Gostimsky (1998) discussed their own data and the data in the literature concerning the chromosomes involved in the seven translocations of Lamm's standard set: "Unfortunately, the incorrectness of chromosome identification in the pea's translocated lines resulted in contradictions in the determination of the chromosomes that participated in the exchanges" (Fujun, Gostimsky, 1998: P. 1269). They did not pay attention to the fact that in most cases there were contradictions between the two numeration systems rather than between different sets of data having some biological sense.

WAITING FOR A SEQUENCED GENOME

At present, with genome sequencing having become almost a routine procedure, the nuclear genome of the pea still remains unread. The irony of the moment consists also in the fact that the genome of the pea aphid *Acyrthosiphon pisum* was sequenced in 2010 (*The International Aphid Genomics Consortium* ..., 2010). This is mostly because the pea genome is quite large—approximately 4.42 pg per haploid genome (Greilhuber and Ebert, 1994), which corresponds to 4.45 billion base pairs (Dolezel and Greilhuber, 2010). For about 40–60% it consists of noncoding repeated sequences (Macas et al., 2007; Novák et al., 2010), with 20–33% belonging just to the *Ogre* retrotransposon from the *Ty3/gypsy* LTR-retrotransposon family (Novák et al., 2010). This will make compilation of the complete genome difficult. Note that the pea genome is quite small compared to that of some related legumes from the Fabeae tribe, such as the broad bean or field vetch, which is manifested in the above-mentioned small size of the chromosomes making the pea an inconvenient cytogenetical object. Thus, the pea genome is too small for cytogenetics but too large for easy full-genome sequencing.

However, the situation is close to being resolved. An international consortium has been launched to sequence the complete pea genome by 2016, the 150th anniversary of the publication of the epoch-making paper by Mendel which gave rise to genetics as a science (Mendel, 1866). For this reason, two libraries of BAC-clones (bacterial artificial chromosomes) were created, of the Cameor commercial cultivar and a wild accession PI269818 (Coyne et al., 2007). The latter was chosen because of its resistance to the viral mosaic (Keller et al., 1998) and *Fusarium* wilt (Smýkal et al., 2012). At the same time, the genome will be sequenced only in the Cameor cultivar. These libraries have already been used for more particular cases: thus, with their aid, two genes used by Mendel were molecularly identified: *a* (Hellens et al., 2010) and *tl* (Hofer et al., 2009).

The pea plastid genome was first sequenced in 2010 (Magee et al., 2010); four years later it was resequenced in five evolutionary distant pea forms (Bogdanova et al., 2015).

Although the complete nuclear genome of the pea remains unavailable, the particular genetics of the pea with the use of molecular markers associated with coding genes is being worked out based on (1) the gene sequences of a related legume species with sequenced full genomes and (2) the available sequences of transcripts of pea genes. Thus, EST-sequences were traditionally used (Gilpin et al., 1997). In recent years, complete transcriptomes have begun to be used for the same purpose, which can be obtained without the reference genome sequence (Franssen et al., 2011; Duarte et al., 2014).

At present, complete genomes have been sequenced in four legume species with small genomes—*Medicago truncatula* (barrel medic, tribe Trifolieae), *Lotus japonicus* (tribe Loteae related to Trifolieae), *Cicer arietinum* (chickpea, tribe Cicereae related to Fabeae), and *Glycyne max* (soybean, tribe Faseoleae). In spite of all these plants belonging to other tribes (although Cicereae is a sister tribe to Fabeae, see Yakovlev, 1991), their genomes demonstrated good synteny to the pea genome (Kaly, 2004; Choi et al., 2004; Aubert et al., 2006; Bordat et al., 2011), while a noticeable synteny can be seen even with the genome of unrelated plants such as the grape, poplar, and papaya. It seems that the genomes of at least all legumes are sufficiently styntenic. This circumstance can be utilised, for instance, for working out CAPS-markers densely covering some sections of the pea's genetic map. For this purpose, the genome of *M. truncatula* (or some other of the above-mentioned species with the available genomes) is sought for ortologs of the pea genes which mark the map section in question and the molecular nature of which is known. Then, the genes are revealed occupying the relevant positions in the barrel medic genome section corresponding to that pea map section. Then, primers are designed based on their primary structure, which are used in PCR reactions with the pea genomic DNA as a matrix. As a rule, the homology of the primary structure of the medic and pea genes is quite high for the primers designed based on the medic genes to allow amplification of the pea gene's fragments. Then the amplified and sequenced fragments of the pea genes are screened for the recognition sites of some restriction endonucleases. Finding them would imply a new molecular marker associated with a coding gene is set in the pea genetic map fragment in question.

Using this approach, F.A. Konovalov et al. (2005) saturated with CAPS-markers the genetic map of the pea linkage group III. V.S. Bogdanova et al., (2012) did the same for small fragments of linkage groups III and V containing genes *Scs1* and *Scs2*, revealed by them as involved in a conflict of the nucleus and plastids in distant crosses of peas. In fact using the same approach—sequencing fragments of pea ortologs of the selected medic genes amplified with the DNA of the parental pea forms involved in the experiment and searching for polymorphism in the obtained sequences, Aubert et al., 2006; Bordat et al., 2011; and Duarte et al., 2014 updated the genetic map with 77, 51, and 730 new markers associated with coding genes, respectively. The number of bridges connecting the genetic maps of barrel medic and pea grew with time swiftly: in 2006–2007 there were 45 (Aubert et al., 2006) and 56 (Choi et al., 2004) of those; in 2011, 140 (Bordat et al., 2011); and in 2014, 1252 (Duarte et al., 2014).

In the work of the French team of 2011 (Bordat et al., 2011) both sources of markers in the pea were fully utilised—sequences of the transcripts of the pea and of the genomes of related species. They analyzed 30156 pea DNA sequences available in the databases to date; their analysis allowed them to recognise sequences referring to 13747 unique genes. For 5460 of them, ortologs were revealed in the genome of *Medicago truncatula*, with 140 of them located in the consensus pea map obtained in the same work. Through the analysis of the synteny of the genomes of the pea, medic, Lotus, soybean, and poplar, the putative positions on the consensus genetic map of the pea were predicted for those 5460 genes. Based on this, an interactive database was created allowing to obtain the presumable position of the map for any pea sequence (http://www.thelegume-portal.net/pea_mtr_translational_toolkit). This approach was called translational genomics. There may be a problem with the translation of this term into Russian, since in English the word "translation" implies the common meaning of translation from one language to another, while in Russian the word "translation" is used only in a molecular biological sense, while another word is used for languages.

Later for the purpose of genetic mapping, the same team obtained the complete pea transciptome (Duarte et al., 2014). They contained transcripts of 68000 genes, of which 41000 were annotated basing on their ortologs in the medic genome; in 35000 among them substitutions were found and 1340 among them were located on the consensus genetic map for the first time.

Somewhat earlier, in 2011, independently of the above-mentioned team and beyond the aim of mapping, transciptomes from different pea tissues containing somewhat more than 80000 genes were obtained by a German-American team (Franssen et al., 2011).

Almost ten years before the transcriptome, the pea proteome began to be analyzed, in particular while studying the ontogenesis of vegetative organs above the ground (Schiltz et al., 2004), regulation of the seed protein content (Bourgeois et al., 2009; 2011), symbiosis with the nitrogen-fixing bacteria (Saalbach et al., 2002), and also resistance to the cold stress (Dumont et al., 2011), powdery mildew (Curto et al., 2006), ascohyta blight (Castillejo et al., 2010), and broomrape (Castillejo et al., 2004).

Among the fashionable modern methods successfully applied to the pea, there are several methods united under another excessively loud term "reverse genetics." "Tilling" is such a approach implemented in the pea (Dalmais et al., 2008) and it includes chemically inducing numerous mutations with the subsequent identification of DNA sites affected by each mutation and phenotyping of the mutant lines obtained. Thus, a researcher may select the mutations in the necessary genes from the whole pool of such lines, get information on these mutations at the DNA level, and evaluate their influence on the phenotype. Until 2012, this set included 4817 lines, for 1840 of which the phenotype was characterised and 464 mutations were identified at the DNA level (Smýkal et al., 2012). Another reverse genetics approach implemented in the pea was virus-induced gene silencing with the use of an early browning virus (Constantin et al., 2004). In particular, with this approach, pea genes responsible for arbuscular mycorrhiza were identified (Gronlund et al., 2010).

Another drawback of the peas as a genetic object is the extreme difficulty of its genetic transformation with agrobacterial plasmids, which has been carried out only in few laboratories in the world (Somers et al., 2003; Svabova et al., 2005).

In general one can see that recently the pea, in spite of some retardation, is at last getting in line with cultivated plants that have been thoroughly studied in term of molecular genetics. Only the last stroke of the sequenced complete nuclear genome is missing. Meanwhile the pea appears at the same level of scrutiny as wheat and, because of the huge genome and amphiploid nature of the latter, most probably will surpass it soon.

SCIENTIFIC FRUITS OF THE PEA

Creation of Genetics

A model genetical object is valuable as an instrument for obtaining fundamental knowledge on heredity rather than itself. The same is true for drosophila, which lacks practical importance (except for causing slight harm in winemaking) but has allowed us to confirm the chromosome theory of heredity, gifted us genetic maps, etc. (Yurchenko et al., 2015). In this respect the input of the pea in fundamental knowledge is unprecedented since its gift was genetics itself as a science, which is known by any schoolboy. In contrast to drosophila, the pea is of great practical importance and thus the progress of its particular genetics is welcome in selection. However, each genetical object has a fundamental value. Which other general biological problems were solved with the aid of the pea?

The study of pea hybrids gave rise not only to genetics but also cytogenetics. As mentioned above, it was this object in which the first translocation in the history of genetics was found (Hammarlund, 1923). However, in cytogenetics, drosophila very soon provided a doubtless advantage, which by a lucky chance happened to possess polytene chromosomes. As a result, the pea for a long time remained underinvestigated in the cytogenetical respect.

Genetics of the Plant-Bacteria Symbiosis

The pea is unique among all other genetical models as it is a well-expressed example of symbiosis between eukaryotes and prokaryotes—symbiotic nitrogen fixation by a symbiotic bacterium *Rhizobium leguminosarum* in special organs of the pea, the root nodules, whose development is, however, induced by the bacterial symbiont. The pea is also capable of forming the arbuscular micorrhyza. Both abilities are shared by all legume plants; however, among them only the pea is a true model genetic object. A vast number of well-known genetic and molecular studies of both participants of this symbiosis in their interaction have been carried out worldwide. In Russia, such studies are conducted under the leadership of I.A. Tikhonovich at the Institute of Agricultural Microbiology, Russian Academy of Agricultural Sciences, and also by K.K. Sidorova with her colleagues at the Institute of Cytology and Genetics, Siberian Branch, Russian Academy of Sciences. Any attempt at reviewing these works would lead to an inadmissible expansion of the volume of this paper; thus here I provide just a reference to a short recent review by the leading world specialists in this subject (Borisov et al., 2011). These studies even resulted in a claim for the creation of a new science—symbiogenetics (Tikhonovich and Provorov, 2012).

Variation of Histone H1 Genes, its Effect on the Phenotype, and its Role in Evolution

The pea turned out to be the best model for the study of phenotypic effects of the variation for an obligatory component of eukaryotic chromatin, histone H1, which was carried out by a team headed by Berdnikov and the results of which are briefly reviewed below. In contrast to the core histones, histone H1 is characterised by significant evolutionary plasticity as it is one of the most variable proteins in eukaryotes. This variation mostly pertains to the positively charged C-terminal hydrophylic domain, which interacts with the negatively charged linker DNA and hence is an important functional part of the molecule. The high rate of variation is in particular provided by the presence in this domain, and also in the pea, of short repeats and motifs apt to generate deletions and duplications (Trusov et al., 2004; Kosterin et al., 2012; Zaytseva et al., 2012, 2015). As an obligatory and at the same time flexible component of eukaryotic chromatin, histone H1 is an element of the molecular environment in which all gene activators and repressors, including specific ones, have to act. Alterations in the H1 molecule structure influencing either the strength of its binding to the DNA or its interaction with other proteins of chromatin (including other, paralogous subtypes of the same histone H1) could have an effect on the differential expression of various genes. Thus, variation of the histone H1 genes could exert an unpredictable effect on the various polygenically determined quantitative traits of an organism, which makes these genes "polygenes of general action" (Berdnikov et al., 1993a, b).

This supposition has been successfully tested in the pea, which turned out to be an ideal experimental model for this. The pea appeared to possess at least seven nonallelic subtypes of histone H1 encoded by unique genes, each of which exhibits allelic variation, detectable even at the level of the electrophoretic mobility of their protein products (Berdnikov et al., 1993a; Kosterin et al., 1994). The most mobile subtype H1-7 is remarkable for its presence only in the chromatin of actively growing tissues, while with the ageing of differentiated tissues their chromatin becomes enriched with the least mobile and most abundant subtype H1-1, and also subtype H1-6 (Kosterin et al., 1994).

Thanks to the fact that the pea was a quite well studied genetical object, these genes were mapped to three genetic loci on two chromosomes, one of them being a cluster of the genes of subtypes H1-2—H1-6 disposed within the limit of 0.1 cM (Rozov et al., 1986; Kosterin et al., 1994). By backcrossing (including the above-mentioned ultra early ripening Sprint-1 line) or selecting one heterozygous plant in subsequent generations, several pairs and series of nearly isogenic lines were created, differing in the allelic variants of some H1 subtypes, which were compared with respect of a number of quantitative traits in uniform greenhouse conditions. As expected, the substitutions of the allelic variants of some subtypes exerted a small but statistically significant effect on some quantitative characteristics of a general nature (Bogdanova et al., 1994, 2007; Berdnikov et al., 1999a). The effects on more specific characteristics, which in the experimental models used referred to the low level of expression of homeiotic genes governing the leaf morphology, appeared even less predictable: ranging from an effect of 20% in the case of the expression of the *tl* locus (normally directing the development of paired organs in the leaf distal domain towards the tendrils) in the hemizygous state (Berdnikov et al., 1999a) to the complete absence of any effect in the case of a leaky mutation *uni*^{tac} of the *uni* locus (normally responsible for the development of a compound leaf with the paired organs on the rachis) (O. Kosterin, unpublished).

The following regularity was traced: the lengthening of the C-terminal domain, and hence an increased affinity to DNA, in subtype H1-7, specific for tissues with actively dividing cells, exerted positive effects on the rate of plant growth (Bogdanova et al., 2007), while the lengthening of this domain in subtype H1-6, accumulating in the chromatin of nongrowing tissues, had a negative effect on the growth rate (Kosterin et al., 2012). A possible interpretation of these observations is quite explicit: an increased presence of H1-7 in the chromatin makes it "younger" as it favors the expression of genes governing the mitotic cycle, while an increased presence of H1-6 makes the chromatin "older," while allelic variants in both subtypes differ in their affinity to the DNA and hence affect their quantity in the chromatin.

A common drawback of the above-mentioned works was the considerable—up to 20 cM—theoretically expected length of the still heterozygous chromosome fragment around histone H1 genes escaping isogenisation, which surely included dozens of unknown genes beyond the histone H1 genes. This drawback has been overcome in experiments using pairs of isogenic lines of relatives of the pea, lentil and grasspea, in which the anomalous H1 allele had a recent mutational origin, so that both the normal and mutant alleles had the same chromosome circumference (Berdnikov et al., 2003a).

Using the pea, the role of histone H1 variation was demonstrated in the course of a "cultural evolution", which is the evolution of a cultivated plant under natural selection in the conditions of traditional, primitive agriculture without conscious selection (Berdnikov et al., 1989; 1993a). In the regional samples of primitive pea landraces, the frequency of one of the allelic variants of the subtype 1 negatively correlated with the accumulated temperature of the vegetation period, so that the samples of northern Russia, Tajikistan, and Afghanistan appeared most enriched with this variant (Berdnikov et al., 1989, 1993a). At the level of the DNA primary structure, it was found that in all the regional samples studied, however distant they were geographically, this variant is encoded by an identical allele, most probably having spread over the Old World with the migration of cultures and supported by natural selection in regions with a cold climate (Zaytseva et al., 2012).

These studies were accompanied by some side results: first, they led to a substantial correction and refinement of the pea's recombination genetic map; second, they contributed to the knowledge on the variation of the histone H1 genes. Thus, in legumes of the Fabeae tribe, the gene of subtype H1-1, whose product comprises about half of the total H1 histone, was found to contain a regular zone coding for a perfect tandem repeat of the pentapeptide Ala-Ala-Lys-Pro-Lys (with substitutions in synonymic positions), the number of copies of which varied due to a phenomenon which the authors called "intragenic conversion" (Berdnikov et al., 2003a; Trusov et al., 2004). It was quite surprising that a substantial intraspecies variation of subtypes H1-1 and H1-6 was not associated with aa comparable interspecies variation in the related *Lathyrus*, *Vicia*, and *Pisum* genera. Hence, the intraspecies variation seems to *de novo* appear in each species within the same quite broad range allowed in the Fabeae tribe (Berdnikov et al., 2003a; Trusov et al., 2004; Kosterin et al., 2012). Third, the histone H1 genes were tested in the pea as a new molecular marker useful for phylogenetic reconstructions (Zaytseva et al., 2012, 2015). The sequence of a minor subtype H1-5 appeared quite informative as having successfully resolved the phylogeny of the *Pisum* genus, notably both at the species and intraspecies levels (Zaytseva et al., 2012), while the gene of subtype H1-7, specific for young tissues, appeared ineffective in this respect, perhaps because of the stronger functional constraints on its product (Zaytseva et al., 2015).

Conflict of the Nucleus and Cytoplasm

A conflict of the nucleus and cytoplasm has been registered in crosses of wild and cultivated forms of *Pisum sativum* L., and also between *P. sativum* and *P. fulvum* Sibth et Smith, usually expressed in the partial sterility of the first generation hybrids, but sometimes having a striking phenotypic manifestation of the underdevelopment of the blade organs, chlorophyllic pigmentation and roots in the first generation hybrids obtained in one of the two reciprocal directions of crosses (Lutkov, 1930; Ben-Ze'ev and Zohary, 1973; Bogdanova and Berdnikov, 2001; Kosterin and Bogdanova, 2015). Bogdanova and colleagues have carried out a detailed genetic analysis of this phenomenon (Bogdanova and Kosterin, 2006; Bogdanova, 2007; Bogdanova and Galieva, 2009; Bogdanova et al., 2009, 2012, 2014), and then a comparative analysis of the plastid genomes (Bogdanova et al., 2015). As a result, this conflict was associated, with a high degree of certainty, with several nuclear genes and one plastidic gene coding for subunits of a very important enzyme complex—the plastidic heteronomic form of acetyl-CoA-carboxylase (Bogdanova et al., 2015), which carries out the first stage of fatty acid biosynthesis. The nuclear gene *Scs1*, being the main actor of the conflict from the side of the nucleus, most probably codes for a biotin and carboxyl carrying protein, while the *AccD* gene, coding for the β-subunit of the carboxyltransferase (Sasaki and Nagano, 2004), participates in the conflict from the side of the plastid. Note that gene *AccD* is characterised by high variability, partly associated with deletions and duplications of short repeated sequences. Some of them may be determinants of the functional interaction with the subunits encoded in the nucleus (Bogdanova et al., 2015).

Thus, for the first time, a case was discovered when a conflict of the nuclear and organellar genomes was associated with the disturbance of the function of a multimeric enzyme complex whose subunits are encoded by different cellular genomes. Earlier such a mechanism of a conflict of the nucleus and cytoplasm had been hypothesised but not found (Burton et al., 2013). As a result, this enzyme complex, plastidic heteromeric acetyl-coA-carboxylase, appeared to be a unique genetical model. On one hand, it allows the reconstruction of the molecular interaction between the subunits by means of genetic analysis, and on the other hand, the structure of the corresponding genes makes it possible to predict the compatibility of the nuclear and cytoplasmatic genes of evolutionarily distant pea forms, which can be important for the involvement of the pea's genetic diversity in breeding.

Origin of B-Chromosomes in Plants

The pea has served as an experimental model for reproducing the initial steps of the origin of supernumerary B-chromosomes in plants according to the hypothesis by Berdnikov, from tertiary trisomics arisingbecause of the incorrect chromosome segregation in the meiosis of heterozygotes for reciprocal translocations (Berdnikov et al., 2003b). The theoretical model implies cross pollination, while the chosen experimental model, the pea, is self-pollinator and hence expectedly has no natural B-chromosomes. However, the experiment involved controlled cross pollination by means of crossing. The hypothesis implied that in small populations, tertiary trisomy could save plants from lethal mutations arising in the genome regions corresponding to the extra chromosome. Later, in the case of the arrest of its crossing over with the chromosomes of the main set, the additional chromosome misses its genetic content because of diploidisation through spontaneous mutations in the surplus gene copies. (Diploidisation implies the average dose of functional alleles of the loci of the genome fragment involved in trisomy approaching 2 with the mutational "switching off" of one of the three alleles initially present in a trisomic.) Based on the Hammarlund translocation producing a small exchange chromosome, a morphological mutation *cri* and specially obtained sporophytic lethals covered by the extra chromosome, a stable, true breeding trisomic pea line Trust was created (Berdnikov et al., 1999b, 2003b). The selection of this line for increased seed production and plant vigor turned out to be very effective (Kosterin et. al., 2008), as implied by the model, assuming that any amorphic or hypomorphic mutation in the genes present in three copies would lead to diploidisation and would decrease the genic imbalance.

The experiment is still going on, with chemical mutagenesis added for acceleration of the diploidisation through induced mutations. The final goal would be to obtain a genetically empty artificial B-chromosome, which would be capable of spontaneously varying its dose in the karyotype. Its saturation with, e.g., genes of resistance to pathogens by means of genetic transformation would turn it into a unique vector capable of accumulating in the karyotype through natural (!) selection operating immediately during cultivation (Berdnikov, unpublished). Note that such a vector can be made based on natural B-chromosomes in objects which have them, e.g., in corn or rye.

Compound Leaf Architectonics

The pea has an imparipinnate compound leaf, whose structure is further complicated by the transformation of the distal paired and terminal unpaired leaflets to tendrils (the loss of the leaf blade and acquisition by the midrib of the ability to coil around the substrate) and the hypertrophy of the leaf-like stipulae, which exceed the leaflets in size. In this the pea has a great advantage over the "plant drosophila", arabidopsis, which has a simple leaf and so cannot serve as a genetical model for studying the genetic basis of the complication of the leaf morphology, which is a characteristic of so many plants, including cultivated ones. The genetic control of the compound leaf architectonics is based on genes which are classified as homeiotic genes, that is, genes switching the developmental program of primordia towards some organ (Gourlay et al., 2000). Thus, mutations tl^w (Blixt, 1972) and *tl2* (Berdnikov, Gorel, 2001, 2005) formally convert tendrils into leaflets. Mutation *af* replaces leaflets with branched tendrils, each corresponding to the distal domain of the normal leaf (Gourlay et al., 2000) (although it is often said that it converts leaflets to tendrils). Mutations *coch* (Ferguson and Reid, 2005; Couzigou et al., 2012), *sil* (Husbands et al., 2003), and especially the combination of mutations *sil* and *ins2* (Berdnikov and Gorel, 2004) convert the stipula into an independent compound leaf with a pair of stipulae and a central rachis bearing paired organs, so that each node gets a whorl of more than one compound leaf. Besides, the same mutation *coch* results in the ectopic appearance of roots on the nodules. Amorphic mutations in all genes controlling the compound leaf development have conspicuous phenotypic manifestations, while their various combinations result in unexpected versions of the morphology going far beyond the normal limits for the Fabaceae family (Blixt, 1972). The combination of mutations tl^w and *ins2* allowed us to recapitulate the bipinnate leaf without tendrils (Berdnikov et al., 2000), which is thought to be ancestral for the Fabales order (Yakovlev, 1991), while mutation *uni* results in the formation of a pseudo-simple leaf (Hofer and Ellis, 1996), among legumes resembling that of *Gueldenstaedtia monophylla* Fisch. Some loci controlling the compound leaf development were for the first time revealed at the Institute of Cytology and Genetics, Siberian Branch, Russian Academy of Sciences during research under the leadership of Berdnikov: *adt* (*air dots*) (Gorel et al., 2002), *ins2* (*insecatus2*) (Berdnikov et al., 2000), and *tl2* (*tendrilless2*) (Berdnikov and Gorel, 2001, 2005).

It turned out that many genes responsible for the compound leaf architectonics are ortologous to the homeiotic genes well known from the developmental genetics of arabidopsis and snapdragon. Thus, the *Uni* gene (*Unifoliata*) responsible for the compound nature of a leaf, namely, for the ability of the meristem leaf to generate paired organs in acropetal sequence, appeared to be an ortolog of *FLORICAULA* in snapdragon and *LEAFY* in arabidopsis—that is of the homeotic genes, whose expression in the apical meristem of these plants turns its development towards a flower instead of a shoot.

Interestingly, this gene directs the leaf development towards a compound type only in representatives of the so-called IRLC-branch of legumes (a group of herbaceous legumes, including the pea, which has lost an inverted repeat from the plastid genome). In this group, the *Uni* gene recaptured this role from the genes of the *KNOTTED1* class, which play this role in other legumes and other plants (Champagne et al., 2007). Gene *Tl* (*Tendril-less*) appeared to be a class 1 homeodomain-containing leucine zipper; expression of the former gene is stimulated by the *Uni* gene, for which purpose it has the so-called motif of binding to *LEAFY* near the initiation point (Hofer et al., 2009). The *Coch* (*Cochleata*) gene is ortologous to the *BOP1* and *BOP2* genes (*BLADE-ON-PETIOLE1-2*) of araidopsis (Couzigou et al., 2012). An amorphic mutation in the *Cri* (*Crispoid*) gene in the pea blurs the limits of the stupulum domain, providing the rachis with wings and additional stipulets at the leaflet bases, and also disturbs the identity of the stipula's adaxial surface. This gene turned out to be ortologous to *PHAN* (*PHANTASTICA*). Expression of this gene is necessary for development of the leaf blade and the identity of its adaxial surface in the snapdragon, tomato, and arabidopsis, but not in the pea (Tattersall et al., 2005).

Interestingly, in the pea, the development of the leaf as a compound depends on the ortolog of *KNOTTED1* and does not depend on the ortolog of *PHAN*, while in the tomato, which also has ortologs of both these genes, the situation is the reverse: it does not depend on the *KNOTTED1* ortolog but does depend on the *PHAN* ortolog. All these results underline a very important circumstance: in different families of vascular plants, similar constructive solutions in leaf architectonics and development are achieved by different interaction schemes of the same set of ortologous homeiotic genes.

The phenotypes observed in studies on genetics of the compound leaf architectonics in the pea are one of the most conspicuous and vivid in developmental genetics. Moreover, they demonstrate a more complicated pattern of gene interaction (in particular, less evident opposition of the cadastre and selector gene functions) than the genes of the famous "ABC of florogenesis"—genetic control of the identity of the flower organs. In the pea this control is identical to that in arabidopsis and snapdgaron, thus supporting the monophily of dicotyledons.

The studies on compound leaf genetics have obtained a surprising and very practically useful application starting from the works by B. Shoad (1974). Thanks to them, many commercial pea cultivars in economically developed countries were recently created on a "leafless" base, having in their genotype recessive mutations *af* (*afila*, "tendrils instead of leaves") and *le* (dwarfism because of the shortened internodes). Mutation *af* replaces the leaflets of the compound leaf with branches of rachis, corresponding to its proximal domain bearing tendrils instead of leaflets. As a result, each leaf bears numerous tendrils on a branched rachis. The effect of the *af* mutation does not spread to the stipula, which is large and leafy in the pea (but not in other legumes, with few exceptions). In such plants, the stipulae are responsible for the main part of the photosynthesis. Their productivity is not affected; besides, the leafless peas have a lower relative mass of straw and are more resistant to draught. However their agrotechnical advantage is crucial: a tangle of twisted tendrils, similar to tumbleweed, forms an elastic and stiff skeleton thanks to which the shoots are directed vertically and do not lodge in the field. The "original sin" of the pea—a weak stem unable to independently support the shoot—was overcome in this way. Many of our compatriots were amazed to see this phenotype when they attempted to grow the pea seeds obtained from the United States.

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